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On Mendelian Dominance

By

A. R. Moore

With 9 figures in text

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UNIV. OF CALIFORNIA

On Mendelian Dominance.

By

Arthur Russell
A. R. Moore. 1882 –
(From the Herzstein Research Laboratory of the University of California, New Monterey, Calif.)

With 9 figures in text.

Eingegangen am 22. Dezember 1911.

Thesis for the doctorate in the U C.
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It is a fact generally recognized that in many cases of hybridization the dominance of Mendelian characters in the heterozygote is incomplete. This incompleteness in development may be permanent and give rise to intermediates; or it may be temporary, obtaining only in the juvenile forms, later giving way to complete dominance of the characters involved.

With a view to getting rational insight into such cases the writer has proposed a biochemical analysis of dominance[1]. The justification for such an assumption is that biologists as a rule accept the fact of a biochemical basis for life phenomena. Thus LOEB[2] very strikingly has shown that the action of the spermatozoon in fertilizing an egg is chemical in character. ROBERTSON[3] has pointed out the fact that the rate of growth of organisms may be interpreted as an autocatalytic reaction.

PHISILAX[4] has proven that the tyrosinase which he found present in the larvae of the cockroach (*Phyllodromia germanica*) gives rise to the pigment of the tegument by oxydizing tyrosin. In the newly hatched larvae the tegument is white but during the following three hours it changes through gray and brown to black. PHISILAX was able to observe the same changes in liquid pressed from the young larvae. He concluded that »the cause of change in color is due to the action of the tyrosinase upon the tyrosin, these two substances existing in the embryo long before development and it is probable that they coexist in the egg or that they are deposited at the time of ovogenesis«. Recently GORTNER[1] has shown in other cases that the pigmentation of the insect larvae is due to the interaction of a chromogen and a member of the tyrosinase group. RIDDLE[2] says »In accounting for melanin color characters I would maintain that we can account for all the major happenings of color development and inheritance with extremely little assumption. It is known that one oxidase is concerned. It is known that the germ possesses actively the power to oxidize amino acids. I think we need make use of nothing in the germ but just this power. It is known that the protoplasm of different species, of different tissues, of different parts of the cell, possess different powers of oxidizing protein bodies. The fate of color characters is then bound up 1) in the union of these particular powers of the two germ cells; 2) in the origin (through other outside developmental processes) of favorable and unfavorable regions for tyrosin oxidations; and 3) in environmental conditions.« BATESON[3] states that »In at least a large number of cases the inheritance of characters consists in the transmission of the power to produce something with properties resembling those of ferments«.

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[1] MOORE, A. R., Univ. of Calif. Publ. Physiology. (1910.) Vol. 4. p. 9—15.

[2] LOEB, J., Chemische Entwicklungserreg. des tierischen Eies. Berlin 1909.

[3] ROBERTSON, T. B., Arch. f. Entw.-Mech. Bd. 25. S. 581 u. f. Bd. 26. S. 108 u. f.

[4] PHISILAX, M. C., Comptes rendus soc. biol. (1905.) Vol. 59. p. 17.

Such facts make reasonable the assumption that something of the nature of an enzyme exists in the germ cell and is vitally concerned in the development of inherited characters. While such definite chemical compounds never have been isolated from the germ cells, the assumption of the existence of such substances does much to unify the many sided results in inheritance experiments as well as to make clear some of the problems of the future. For the sake of convenience, then, let us call these substances enzymes. Since we know precisely many of the laws governing chemical reactions in vitro, our theory enables us to explain, if not to predict, the results of chemical reactions concerned in fertilization and development.

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[1] GORTNER, R. A., Journ. of Biol. Chem. (1910.) Vol. 7. p. 365. (1911.) Vol. 10. p. 89.

[2] RIDDLE, O., Biol. Bulletin. (1908.) Vol. 16. p. 339.

[3] BATESON, W., MENDEL's Principles of Heredity. (1909.) p. 268.

Therefore, accepting the presence and absence hypothesis and adopting a biochemical theory of inheritance, we may say that each germ cell from the dominant parent contains a full amount of the enzyme underlying the development of the dominant characters while the germ cells of the recessive contain none. The hybrid resulting from the cross between these two parents would have but one half the normal amount of enzyme necessary for the development of the dominant characters. Now the velocity of a chemical reaction depends upon the concentration of the reacting substances and in enzyme reactions varies directly as the concentration or as the square root of the concentration of the enzyme. The final equilibrium in enzyme reactions in most cases is unaffected, in other cases it bears some relation to the concentration of the enzyme 1).

If these laws are operative in the development of organisms, then in our hypothetical F_1 individual, the dominant character should appear more slowly than in the pure dominant strain, although final equilibrium may be the same. The perfect development of dominant characters may be inhibited 1) by the cessation of reactions upon the products of which such characters depend for their full development. Thus the vegetative growth of many plants ceases when sexual products are formed. 2) The equilibrium of the reaction may be affected by the concentration of the enzyme. In either of these two cases the development of the dominant character will not be complete and as a result we shall have only intermediate dominance.

Now the rate of development of a dominant character in the heterozygote may be retarded but the process finally reaches perfect equilibrium so that the heterozygote cannot be distinguished from the pure dominant. Perhaps the best illustration is in the case of LANG's 2) experiment with snails. In these experiments LANG crossed red and yellow parents. In the F_2 generation, when the animals were young, the heterozygotes were yellow so that the ratio appeared 3 yellow: 1 red. As they grew older the red pigment developed in the heterozygotes and at maturity the ratio was 3 red: 1 yellow 3).

---

1) TAYLOR, A. E., Journ. Biol. Chem. (1910.) Vol. 8. p. 503.

2) LANG, Über die Bastarde von *Helix hortensis* Müller und *Helix nemoralis* L. Eine Untersuchung zur experimentellen Vererbungslehre. (1908.) Jena.

3) SHULL uses this example to explain the apparent dominance of absence over presence and concludes that in such cases the positive character is only latent in the heterozygote. Am. Naturalist. (1909.) Vol. 43. p. 410.

To turn to a more familiar example of the working out of this hypothesis, we may note the inheritance of hair and eye pigment in the human species. Young children who are the result of a cross between a blond and a brunette usually are blonds but develop more hair and eye pigments later in life. In the children of two brunettes hair and eye pigments appear strongly in infancy.

It occurred to me that a phenomenon of the same nature might be observed in the development ot the larvae of the two Pacific Coast sea urchins (*Strongylocentrotus purpuratus* and *S. franciscanus*) and their hybrids. In preparing the cultures much the same precautions against contamination with the wrong sperm were used as last year¹), viz: a pipette was not used a second time until after it had been cleaned with fresh water and dried. The eggs of but one female of each species were used for purposes of comparison. The cultures of one set were all started at the same time. I did not study the *F*♀ × *P*♂ hybrids because such larvae, with few exceptions, are pathological. As soon as the blastulae came to the surface of the water they were pipetted off and put into a finger bowl containing 50 cc. of sea water. About forty-eight hours after fertilization

Fig. 1.

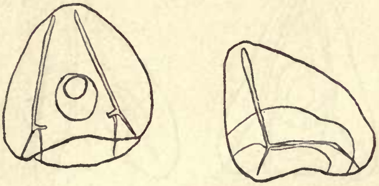


Fig. 2.

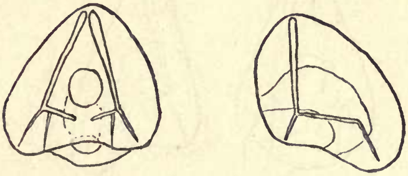
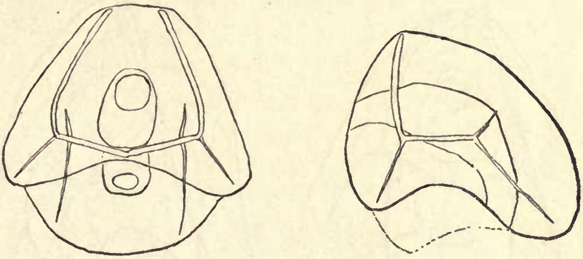


Fig. 3.



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¹) Loeb, J., King, W. O. R., and Moore, A. R., Arch. f. Entw.-Mech. Bd. 29, S. 354.

(Temp. 16°—18°C) the skeletons began to be deposited and soon the larvae assumed the characteristic pluteus form (Figs. 1, 2, and 3).

Loeb, King, and Moore have shown that the spininess of the skeleton, early development of arms, cross bars and dome shaped body, all *S. franciscanus* characters, are dominant over the smooth skeleton, lack of cross bars, short arms and pyramidal form of the *S. purpuratus*. My plan was carefully to record the development of the larvae from day to day and determine whether the dominant characters appeared in the hybrid plutei as soon as in the pure culture. I have followed through five sets of experiments. Each experiment contained thousands of larvae. I find, in all cases, that the development of the dominant characters — such as spininess, length of arms, and body shape — is retarded in the heterozygote. I had at first supposed that the amount of cross-bar formed might be a reliable index to the rate of development of the dominant characters. This, however, is not true, because in some cases I found the cross bar fused in the hybrid plutei on the third day while in other cases it had entirely failed to fuse on the fifth. This is due to the fact that the enlargement of the gut pushes the skeleton

Fig. 4.

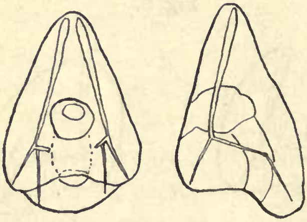


Fig. 5.

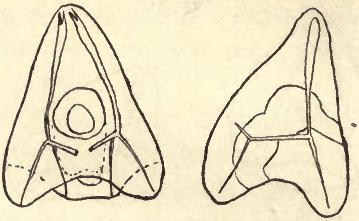
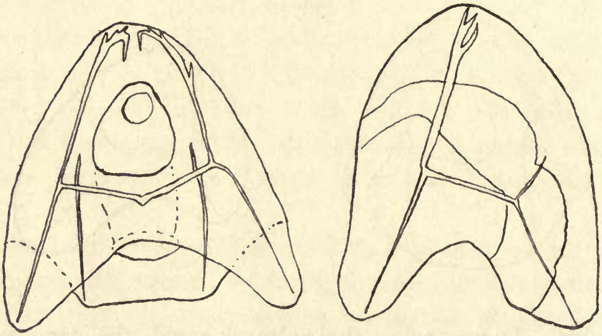


Fig. 6.



apart to a greater degree in some cases than in others. A large number of drawings with the camera lucida were made each day. For the sake of clearness I have given in the figures illustrating this paper, drawings of but two representative plutei of each culture each day. These are drawings made with camera lucida. They therefore show the relative size of *franciscanus* and *purpuratus* larvae.

A comparison of the juvenile plutei (Figs. 1, 2, and 3) shows the hybrid to differ very little from the pure *purpuratus* except for the cross-bars in the former. The pure *franciscanus* larvae are more advanced in the development of arms but otherwise the shape differs scarcely at all from Figs. 1 and 2. By the beginning of the fourth day the *franciscanus* plutei (Fig. 6) have attained complete development both as to spininess, length of arms, and body shape. The hybrid (Fig. 5) only occasionally has spines at this stage, the arms are somewhat longer than the pure *purpuratus* (Fig. 4) but the body shape is much the same. Twenty-four hours later the *franciscanus* plutei (Fig. 9) have the same form as on the day before, but the hybrid (Fig. 8) shows slightly longer arms, a body shape more like

Fig. 7.

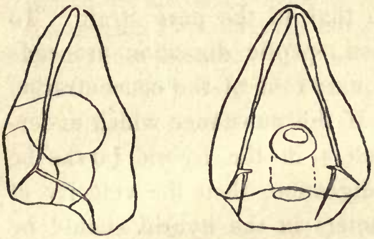


Fig. 8.

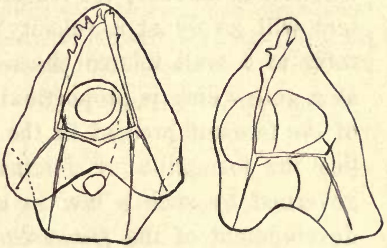
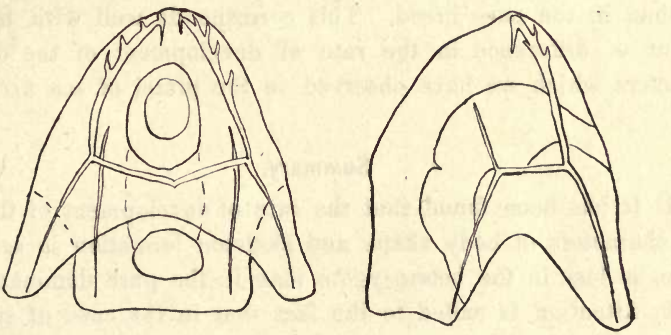


Fig. 9.



that of *franciscanus* than that of the *purpuratus* (Fig. 7), and a marked increase in spininess of the skeleton.

The whole case may be summed up by saying that the *franciscanus* characters are retarded in their development in the hybrid, just as is the development of red pigment in Lang's heterozygote snails. As we have stated, such a result is susceptible of explanation if we consider development of the characters of an organism as due to chemical reactions. Since the substance which produces the characters of *franciscanus* is present in the hybrid in one half the normal amount, the reactions involved in producing these characters will go on at a velocity less than that in the pure strain. To refer to a well known chemical reaction, peptic digestion proceeds at a rate which is proportinal to the square root of the concentration of the ferment present in the system. If this substance which underlies the formation of dominant characters in the hybrid larvae be governed by such a law as is peptic digestion, then the velocity of development of the *franciscanus* characters in the hybrid should be seven-tenths that in the pure *franciscanus*, since the ratio is $\sqrt{1} : \sqrt{1/2}$. Therefore, the rate of the reaction in the hybrid is only slightly less than in the pure breed. This corresponds well with the small amount of difference in the rate of development of the dominant characters which we have observed in the plutei of sea urchins.

Summary.

1) It has been found that the rate of development of the dominant characters of body shape and skeleton formation in sea urchin larvae, is less in the heterozygote than in the pure dominant.

2) Attention is called to the fact that in the case of snails investigated by Lang the rate of development of the dominant color is less in the heterozygote than in the pure dominant.

3) According to our hypothesis that the substances underlying the formation of dominant characters obey the laws governing enzyme reactions, we should expect these reactions to go forward at a slower rate in the heterozygote than in the pure dominant because the former contains but one half the amount of enzyme to be found in the latter.

In conclusion I wish most heartily to thank Prof. S. S. Maxwell and Prof. T. B. Robertson for the helpful interest they have shown during the preparation of this work.

Zusammenfassung.

1) Es fand sich, daß der Entwicklungsbetrag der Dominantencharaktere in Körpergestalt und Skeletbildung bei Seeigellarven für den Heterozygoten geringer ist als für den reinen Dominanten.

2) Die Aufmerksamkeit wird auf die Tatsache gelenkt, daß in dem Falle der von Lang untersuchten Schnecken der Entwicklungsbetrag der Dominantenfarbe beim Heterozygoten geringer ist als beim reinen Dominanten.

3) In Übereinstimmung mit unsrer Hypothese, daß die der Bildung von Dominantencharakteren unterworfenen Substanzen den Gesetzen gehorchen, welche die Enzymreaktionen beherrschen, sollten wir erwarten, daß diese Reaktionen beim Heterozygoten mit geringerer Geschwindigkeit vor sich gehen als beim reinen Dominanten, weil der erstere nur die Hälfte soviel Enzym enthält, wie im andern zu finden ist.

(Übersetzt von **W. Gebhardt.**)

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